Flexural and Torsional Stiffness in Multi-Jointed Biological Beams

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Abstract. Flexibility, the ability to deform in response to loads, is a common property of biological beams. This paper investigates the mechanical behavior of multi-jointed beams, which are characterized by a linear series of morphologically similar joints. Flexural stiffness and torsional stiffness were measured in two structurally distinct beams, crinoid arms (Echinodermata, Comatulida) and crustacean antennae (Arthropoda, Decapoda). Morphological data from these beams were used to determine the relative contributions of beam diameter and joint density (number of joints per millimeter of beam length) to the flexural and torsional stiffness of these two structures. As predicted by beam theory, beam diameter influenced stiffness in both crinoid arms and crustacean antennae. In crinoid arms, increases in joint density were associated with decreases in stiffness, but joint density had no significant influence on stiffness in crustacean antennae. In both crinoid arms and crustacean antennae, the magnitudes of flexural and torsional stiffness, as well as the ratio of these two variables, were similar to previously reported values for non-jointed biological beams. These results suggest that the structural design of a biological beam is not a limiting factor determining its mechanical properties.

Introduction

Biological beams, which are structures that are long relative to their width, can be divided into three broad groups based on their structural design. *Continuous beams* have no distinct discontinuities in either material or geometry along the length of the beam. These continuous beams, such as leaf petioles and tree trunks, deform relatively evenly along their entire length when loaded. Continuous beams contrast with *jointed beams*, which are characterized by one or a few material or structural discontinuities along their length which allow the beam to deform at particular points. Examples include vertebrate limbs and arthropod appendages. The third structural design is a *multi-jointed beam*, which is characterized by a linear series of morphologically similar joints connected by a series of stiff elements. The vertebrate backbone is the most extensively studied example of a multi-jointed beam (see Gál, 1993; Long *et al.*, 1997); other examples are found in echinoderms (Baumiller and LaBarbera, 1993), cnidarians (Muzik and Wainwright, 1977), and plants (Niklas, 1997).

When loaded, a multi-jointed beam will deform at each of the joints. Yet, because the joints are arrayed in a linear series, the deformation is evenly distributed along the length of the beam. Thus, the overall deformation of the beam resembles that of a continuous beam, although the underlying mechanism (deformation at individual joints) differs dramatically. Ideally, studies of the mechanical properties of a multi-jointed beam should include information on the overall flexibility of the beam as well as on the relative contribution of the individual joints.

Regardless of their structural design, most biological beams are flexible; that is, they deform in response to loads (Vogel, 1984; Denny, 1988). One dictionary (*New Lexicon Webster's Dictionary,* 1987) defines flexibility as the quality of being easily bent, and rigidity as the quality of resisting deformation. These two contrasting states actually reflect a continuum that can be described with a single, more precise term borrowed from engineering beam theory. Stiffness is defined as a mechanical property indicating the resistance of a material or structure to deformation under a given load (Roark, 1943). Flexural stiffness is a measure of the resistance of a structure to bending, and torsional stiffness is a measure of the resistance of a structure to twisting (Roark, 1943).

Flexural stiffness and torsional stiffness are composite variables whose magnitudes are determined both by material and structural properties (Wainwright *et al.*, 1976). Flexural stiffness is expressed as EI, where E is Young's modulus of elasticity and I is the second moment of area relative to the neutral plane of bending (*i.e.*, the plane that neither shortens nor lengthens during deformation). Torsional stiffness is expressed as GJ, where G is the shear modulus and J is the polar moment of area about the central axis of rotation. I and J reflect the cross-sectional geometry of a beam and are influenced by both size and shape. Size is a very strong determinant of beam stiffness (Roark, 1943; Wainwright *et al.*, 1976), as both I and J are proportional to radius to the fourth power.

Flexural stiffness and torsional stiffness are engineering terms used to describe the stiffness of ideal beams that meet a certain set of criteria (Roark, 1943), none of which are met by either continuous or multi-jointed biological beams (Wainwright *et al.*, 1976). For biological beams, flexural stiffness and torsional stiffness are descriptors of the overall mechanical behavior of the beam, reflecting the amount of deformation observed under a given load. As such, the presence of joints does not negatively impact the overall usefulness of these terms as a means to quantify the stiffness of biological beams.

The stiffness of biological beams can also be characterized by the dimensionless, and thus size invariant, ratio EI/GJ, called the twist-to-bend ratio (Niklas, 1992; Vogel, 1995; Etnier and Vogel, 2000). The twist-to-bend ratio indicates the relative resistance of a beam to bending *versus* twisting, without reference to the absolute magnitude of either. Intuitively, a higher twist-to-bend ratio indicates a structure that twists more readily than it bends. Previous studies have found that the twist-to-bend ratio is a biologically relevant parameter that provides insight into the functional demands on a structure. For example, daffodil stems (Etnier and Vogel, 2000), leaf petioles (Vogel, 1992), and sedges (Ennos, 1993) are characterized by relatively high twist-to-bend ratios. These structures easily twist into low-drag configurations when the wind blows, thus reducing the potential for damage to the organism.

In this paper, values for flexural and torsional stiffness, as well as the twist-to-bend ratio, are reported for crinoid arms (Echinodermata, Comatulida) and crustacean antennae (Arthropoda, Decapoda). Mechanical and morphological data from these beams are used to determine the relative contributions of beam diameter and the number of joints to the flexural and torsional stiffness of these two structures. This broadly comparative study of morphologically distinct structures provides insight into the contribution of a serial arrangement of joints to the mechanical properties of multi-jointed beams.

Comatulid crinoids have long, slender arms composed of a linear series of ossicles connected by muscles and ligaments (Breimer, 1978). The arms move actively in response to muscular contractions (Breimer, 1978) or passively in response to external forces. Crinoids extend their arms into the currents to filter feed passively (Liddell, 1982), thus the arms must be flexible enough to be positioned for feeding, yet stiff enough to maintain that position once obtained (Meyer, 1971). The flexibility of the arms is also relevant during locomotion (Motokawa, 1988), because the arms are bent during swimming and crawling (Breimer, 1978; Shaw and Fontaine, 1990). The dependence of feeding and locomotion on the mechanical properties of the arms suggests that these properties are important to the survival and reproductive success of comatulid crinoids. The only experimental studies of arm mechanics have explored the behavior of isolated joints in the arm (Birenheide and Motokawa, 1994, 1996) without considering how the serial arrangement of the joints affects the mechanics of this multi-jointed beam.

The second antenna of a lobster or crayfish consists of a series of calcified rings, or annuli, connected by flexible arthrodial membranes (Tautz *et al.*, 1981). There are no muscles associated with the annuli of the antennae, although the entire structure can be moved by muscles located at its base (Sandeman, 1985). Hair receptors on each annulus are sensitive to gross water movements, water vibrations, and mechanical deformation of the antenna (Vedel, 1985). In palinurid lobsters, the antennae are not only used as sense organs, but are also actively used as a defensive mechanism to ward off predators (Atema and Cobb, 1980). These two functions may have conflicting mechanical demands in lobsters, because the antenna must be flexible enough to deform in response to water vibrations, but also stiff enough to serve as a defensive weapon. Again, very little is known about how the multi-jointed nature of these beams affects their mechanical properties.

Materials and Methods

Specimens

Crinoids. Specimens of *Comactinia echinoptera* were obtained from the invertebrate collection at Duke University Marine Laboratory, Beaufort, North Carolina, and freshly preserved specimens of *Florometra serratissima* were obtained from Sea Life Supply in Sand City, California. Both species were initially preserved in formalin, and then stored in 70% alcohol. Prior to testing, arms were disarticulated proximally and then transferred through a series of increasingly dilute alcohol solutions, culminating in seawater.

Crustaceans. Specimens of *Procambarus sp.* (freshwater crayfish) were obtained commercially from a local grocer (Wellspring Grocery), and specimens of *Panulirus argus* (spiny lobster) were obtained from investigators at the University of North Carolina, Chapel Hill. Antennae were disarticulated from the carapace and frozen until tested. The
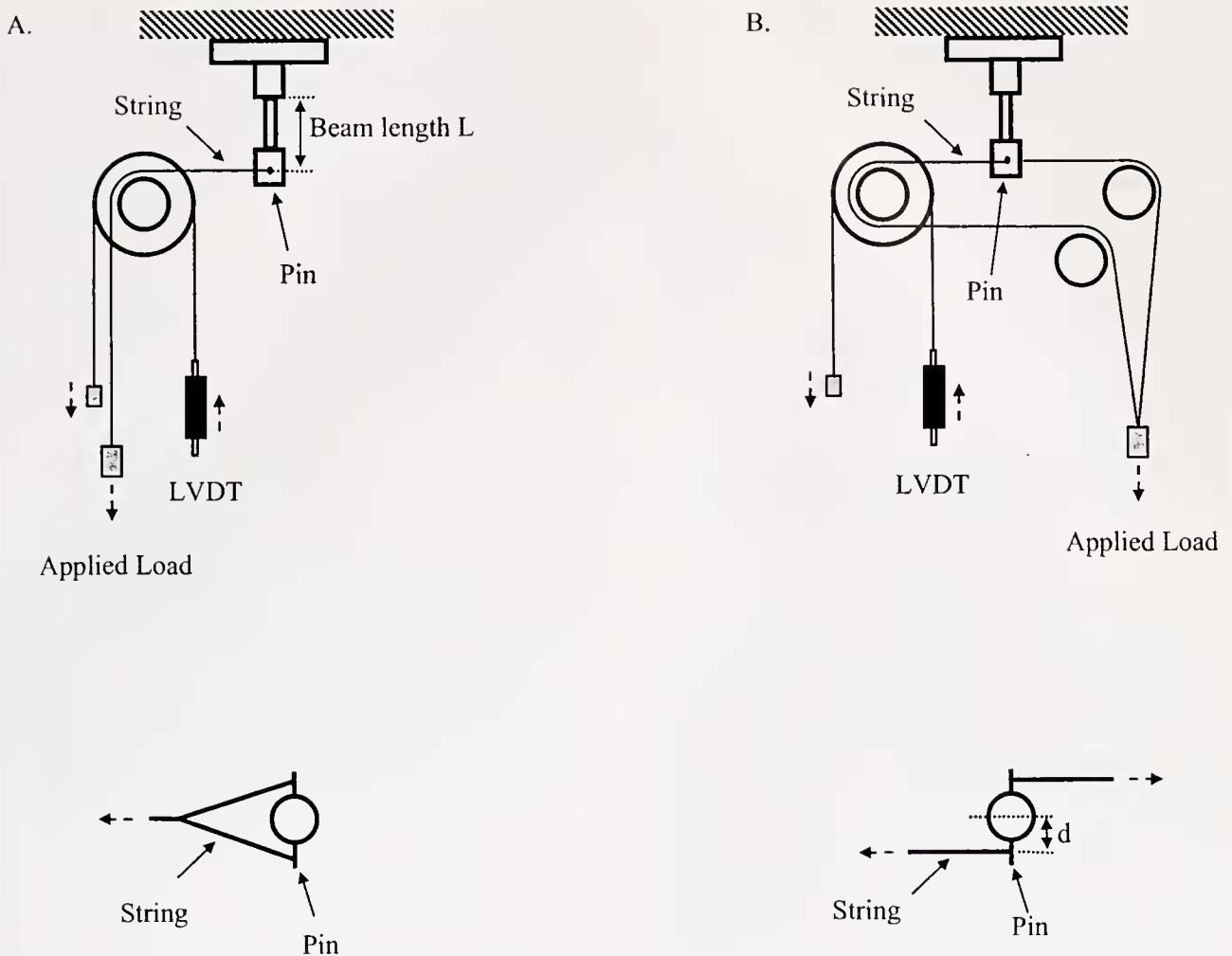
Figure 1. Mechanical apparatus for measuring flexural and torsional stiffness. (A) Flexural stiffness is measured by applying a load to the specimen's free end, causing it to bend. The two pulleys on the left are coaxial. Shown below is a cross section through the free end of the embedding cap, illustrating how the load is applied during flexural tests. (B) Torsional stiffness is measured by applying a load to the specimen's free end, causing it to twist. Shown below is a cross section through the free end of the embedding cap, illustrating how the load is applied during torsional tests. The load is applied simultaneously to the two ends of pin extending through the embedding cap, causing the specimen to twist, but not bend. L = Beam length. d = moment arm. LVDT = linear variable differential transformer. (Based on Vogel, 1992.)

antennae were thawed in seawater or fresh water, as appropriate, before testing.

Mechanical measures

For both flexural and torsional stiffness, the free ends of the specimen were embedded in hard, plastic caps (diameter approximately 11 mm, length 15 mm) with 5-minute epoxy resin. As the epoxy cured, a pin was inserted in the distal cap. The proximal end of the prepared specimen was fixed in place. A load was applied to the pin at the free distal end, causing the specimen to bend or twist (Fig. 1). Through a series of pulleys and strings, the deformation of the specimen was linked to movement of a linear variable differential transformer (LVDT, Pickering 7308-W2-AO), which provided a voltage output proportional to distance traveled (see Vogel, 1992, for full details). The LVDT was calibrated with a micrometer, and each reading was corrected for load-dependent stretching of the string (Berkley Gorilla Braid 10-lb-test fishing line made of braided gelspun polyethylene fibers). All readings were taken on moist specimens 60 s after loading, to allow for initial creep. Specimens were tested with two loads of different magnitude, and data for deformation relative to the load were averaged. This experimental protocol assumes that flexural and torsional stiffness are linear functions of load.

Flexural stiffness (in $N \cdot m^2$) was calculated with the usual formula for end-loaded cantilever beams:

$$\text{Flexural stiffness} = \frac{FL^3}{3y} \qquad (1)$$

where F is the force applied, L is the length of the beam, and y is the deflection at the free end of the beam (Fig. 1A). The formula is satisfactory for deflections up to about 10% of total specimen length (Gere and Timoshenko, 1984). Crinoid arms and crustacean antennae are radially asymmetric, so flexural stiffness was measured both dorsoventrally (oral/aboral) and laterally. These values were then averaged to provide an overall measure of the flexural stiffness of the system.

Torsional stiffness (in $N \cdot m^2$) was determined by applying a load to the distal end of the beam, causing the specimen to twist (Fig. 1B). Calculations of torsional stiffness were based on the following formula:

$$\text{Torsional stiffness} = \frac{Fd}{\theta/L} \qquad (2)$$

where F is the force applied at a moment arm d, L is the length of the beam, and θ is the resulting rotation in radians.

A test of the apparatus using a piece of spring steel (0.65 mm in diameter) gave an average EI/GJ value of 1.4 (standard deviation 0.3), close to the expected value of 1.3 (Gere and Timoshenko, 1984). This error indicates a systematic overestimate of about 8% in the ratios given here.

In some cases, the applied loads were so small that they did not overcome the frictional resistance of the pulleys in the test apparatus. For measures of flexural stiffness, data were omitted if (1) the total deflection was less than 1% of the total specimen length, and (2) the load applied over the moment arm of the pulley was less than or equal to 4.9×10^{-3} N (0.5 g). For torsional measures, data were omitted if (1) the total rotation was less than 0.06 radians (3.6°), and (2) the load applied over the moment arm of the pulley was less than or equal to 9.8×10^{-3} N (1 g).

Morphological measures

Immediately after the mechanical tests, beam length (L) and moment arm (d) were measured using digital calipers (resolution 0.1 mm). The beam diameter was recorded as the average diameter of the specimen at the midpoint of the beam. The number of joints in each specimen was counted to calculate joint density (number of joints per millimeter of beam length).

Data analysis

The average twist-to-bend ratio for each species was calculated from the twist-to-bend ratio for each individual. Distributions and variances were normalized using log-transformed values for flexural stiffness, torsional stiffness, the twist-to-bend ratio, and beam diameter (Sokal and Rohlf, 1981). Joint densities were unaltered because of their normal distribution. Student's t tests were used to determine whether there were significant differences in these variables within the crinoids and within the crustacea. Differences between phyla were not tested because distinct preservation methods were used for crinoids and crustaceans.

Morphological and mechanical data from the two species of crinoids and the two species of crustaceans were combined to provide information on the general structural design of each system. Although there are assuredly mechanical and morphological differences within each phylum, these are assumed to be relatively minor compared to the differences between the two. Multiple regressions were used to determine the relative contribution of beam diameter and joint density to flexural and torsional stiffness (Sokal and Rohlf, 1981). Multiple regressions determine whether a linear combination of independent variables explain a significant portion of the variability observed in the original data (Sokal and Rohlf, 1981). Additionally, multiple regressions indicate which of the independent variables contribute significantly to the overall model.

Because of the unequal variances of these data, differences in joint density between crinoid arms and crustacean antennae were examined using a Wilcoxon rank sum test for nonparametric data (Glantz, 1992).

Microsoft Excel 5.0 (1995) was used for all data manipulation, and JMP In (SAS Institute, Inc., Cary, NC) was used for all statistical analyses.

Results

Mechanical measures

Flexural stiffness and torsional stiffness varied greatly from specimen to specimen, as expected based on differences in beam diameter between individuals (Table 1). The coefficients of variation for flexural stiffness ranged from 84% to 196%, whereas those for torsional stiffness ranged from 61% to 110%. The twist-to-bend ratio was also highly variable (Table 1), with coefficients of variation ranging from 41% to 88%. The variability of the twist-to-bend ratio far exceeded that of the test apparatus, suggesting that the variability was real. The magnitudes of flexural stiffness and torsional stiffness varied among all of the species. *Procambarus* was the most flexible beam in both bending and twisting, and *Panulirus* was by far the stiffest in both measures. The two crinoids fall in the middle, with *Florometra* being stiffer than *Comactinia*. This pattern was not observed in the twist-to-bend ratio, where *Panulirus* had the lowest ratio and *Florometra* had the highest. The values for flexural stiffness, torsional stiffness, and twist-to-bend ratio are comparable to those of other continuous biological beams (Table 2), such as leaf petioles and plant stems.

Table 1

Morphological and mechanical values for multi-jointed beams

Species	n	Diameter (mm)	Flexural stiffness (N · m^2 × 10^{-6})	Torsional stiffness (N · m^2 × 10^{-6})	Twist-to-bend ratio
Comactinia echinoptera	10	1.33 (0.13)	50 (47)	15 (11)	4.3 (3.8)
Florometra serratissima	6	1.75 (0.10)	392 (383)	51 (31)	6.6 (2.7)
Procambarus sp.	8	0.99 (0.07)	25 (21)	6 (4)	4.5 (3.7)
Panulirus argus	13	2.83 (0.36)	5827 (11466)	2036 (2242)	1.8 (1.3)
			n = 12		n = 12

Mean values for beam diameter, flexural stiffness, and torsional stiffness for *n* specimens. In one case, as noted, the number of specimens varied. The mean twist-to-bend ratio is the average calculated from the individual twist-to-bend ratios. The standard deviation for each parameter is given in parentheses.

Mechanical differences between crinoid species

The arms of *Florometra* had significantly higher flexural ($t = -3.88$, $P < 0.002$) and torsional ($t = -3.40$, $P < 0.004$) stiffness than those of *Comactinia* (Table 1). These differences may be associated with differences in the size of the two species, because both flexural and torsional stiffness are highly size dependent. *Florometra* specimens had significantly thicker arms (Table 1) than *Comactinia* specimens ($t = -2.27$, $P < 0.04$). Despite the differences in the magnitudes of flexural and torsional stiffness, the twist-to-bend ratios of these two species were not significantly different ($t = -1.70$, $P < 0.112$).

Mechanical differences between crustacean species

Panulirus antennae were significantly stiffer in flexural ($t = -5.63$, $P < 0.0001$) and torsional ($t = -7.99$, $P < 0.0001$) stiffness than *Procambarus* antennae (Table 1). Again, these differences may be associated with size, because *Panulirus* antennae were significantly larger in diameter (Table 1) than *Procambarus* antennae ($t = -5.05$, $P < 0.0001$). The twist-to-bend ratio of *Panulirus* was significantly higher than that of *Procambarus* ($t = 2.43$, $P < 0.026$). As in the crinoid arms, the magnitudes of

flexural and torsional stiffness varied between species, but in this case, the twist-to-bend ratios also differed.

Differences between structural designs

Morphology. Joint density differed significantly ($Z = 3.28$, $P < 0.001$) between the crinoid arms and crustacean antennae. Crustacean antennae had an average joint density of 2.04 mm^{-1} (SD = 1.18), whereas crinoid arms had an average joint density of 0.82 mm^{-1} (SD = 0.17). These results correspond to about 200 joints in a 10-cm-long crustacean antenna, but only about 80 joints in a crinoid arm of the same length.

Mechanics. In crinoids. the multiple regression model accounted for a significant portion of the observed variation in both flexural ($R^2 = 0.87$) and torsional ($R^2 = 0.74$) stiffness. Both joint density and diameter contributed significantly to the overall model. Increases in diameter were associated with increases in stiffness, and increases in joint density were associated with decreases in stiffness (Table 3). In crustacean antennae. the model also explained a significant portion of the observed variation in flexural ($R^2 = 0.92$) and torsional ($R^2 = 0.91$) stiffness, although in this case, only beam diameter contributed significantly to the overall model (Table 3). Joint density did not contribute significantly to either flexural or torsional stiffness in the crustacean antennae (Table 3). In summary, beam diameter was an important determinant of stiffness in both multi-jointed beams, as expected for a continuous beam. Joint density, which was expected to affect the mechanical properties of multi-jointed beams, was a determining factor only in the crinoid arms.

Table 2

Mechanical properties of biological beams

Biological beam	Flexural stiffness (N · m^2 × 10^{-6})	Torsional stiffness (N · m^2 × 10^{-6})	Twist-to-bend ratio
Daffodils[1]	11900	890	13.3
Sweet gum petiole[2]	984	199	5.1
Sunflower shoot[2]	73	53	1.4

Mean flexural stiffness, torsional stiffness, and twist-to-bend ratios for a variety of continuous biological beams.
[1] Data from Etnier and Vogel (2000).
[2] Data from Vogel (1992).

Discussion

The results of this study suggest that flexibility in multi-jointed beams is influenced by variables associated with both continuous and jointed beams. As predicted by engineering beam theory, beam diameter contributes to flexural and torsional stiffness in both crinoid arms and crustacean

Table 3

Factors affecting stiffness

			Model for log (stiffness)	Regression coefficients	
Structural design	n	R^2	P values	log (diameter)	Joint density
Flexural stiffness					
Crinoids	16	0.87	0.0001*	2.4*	−2.5*
Crustaceans	15	0.92	0.0001*	4.0*	0.0
Torsional stiffness					
Crinoids	16	0.74	0.0002*	2.1*	−1.3*
Crustaceans	15	0.91	0.0001*	4.4*	0.1

Statistical values for multiple regressions of log (diameter) and joint density against log (stiffness) for both structural designs (n = sample size). The model tests the significance of the overall regression equation, which is in the form $Y = A + BX_1 + CX_2$. Values given for log (diameter) and joint density are standard partial regression coefficients for flexural and torsional stiffness. Regression coefficients that contribute significantly to the overall model ($P < 0.05$) are marked with asterisks. For example, in crustaceans, the linear equation, log $(EI) = a + 4.0*$log (diameter) + 0.0*joint density, explained 92% of the observed variation in flexural stiffness. Joint density, with a regression coefficient of 0.0, did not contribute significantly to the model.

antennae. In contrast, joint density contributes to beam stiffness only in the crinoid arms. Future studies of multi-jointed beams must consider both types of variables to fully understand the mechanical properties of these structures.

The flexibility of crinoid arms is influenced both by beam diameter and by joint density, so morphological variation at the level of the entire arm or at the level of the individual ossicles will affect the mechanical properties of the arms. This result is particularly interesting because the evolutionary success of the comatulid crinoids has been attributed to morphological changes that increased arm flexibility relative to the stalked crinoids (Meyer and Macurda, 1977). Increased arm flexibility, coupled with the loss of a stalk, enabled comatulid crinoids to become secondarily mobile (Motokawa, 1988). Today, this mobility allows comatulids to feed in variable water currents and to move in response to undesirable environmental conditions or predators (Meyer and Macurda, 1977). The hypothesis that comatulid crinoid arms are more flexible than stalked crinoid arms could be directly tested in extant crinoids by using the techniques developed in this study. Similarly, arm diameter and joint density may serve as useful proxies for investigating flexibility in fossil specimens, providing valuable insight into changes in arm flexibility over evolutionary time.

The mechanical properties of crinoid arms may determine, in part, the distribution of individuals in the environment. Comatulid crinoids differentially distribute themselves on the basis of flow regime, with some species preferring exposed sites with relatively predictable flows and others preferring more sheltered areas, with unpredictable flow (Meyer, 1973a). *Comactinia* is typically found in the infrastructure of the reef in sheltered areas (Meyer, 1973b). Its arms bend and twist relatively easily, potentially allowing the animals to adjust to flows that change in both velocity and direction. In contrast, *Florometra* tends to be found at the apex of rocky outcroppings (Shaw and Fon-

taine, 1990) where it is exposed to more regular flow (LaBarbera, 1982). The arms of *Florometra* are stiffer in both bending and twisting than those of *Comactinia*. The flexibility needed to respond to constantly changing flows may not be necessary in a steady current. Instead, the arms may simply need to be stiff enough to maintain their position. Because stiffness is related to arm diameter, these results also suggest that individuals within a species may be differentially distributed on the basis of their size. Larger individuals, with stiffer arms, may be able to live and feed in different areas than smaller, more flexible, individuals. These results suggest that the mechanical properties of crinoid arms may be tuned to the specific loading regime of the animal's preferred habitat.

Although the magnitudes of flexural and torsional stiffness differed between these crinoid species, there were no detectable differences in their twist-to-bend ratios. This constancy suggests that there is a functional advantage to maintaining the relationship between flexural and torsional stiffness across comatulid crinoid species, although the biological relevance of this constancy has yet to be determined. One possibility is that the constant twist-to-bend ratio reflects selective pressure on the ability to passively orient the arms with respect to water currents during feeding. The ability to passively orient the arms may be particularly important for crinoids that live where flow oscillates continuously. Passive orientation of entire organisms has been described in gorgonian corals (Thèodor and Denizot, 1965; Wainwright and Dillon, 1969) and in stalked crinoids (Baumiller and Plotnick, 1989), although the mechanisms differ in these two systems. In comatulid crinoids, passive orientation has been observed in the individual pinnules radiating off of each crinoid arm (Baumiller and Meyer, 2000), suggesting that the mechanical properties of the arms may be less important than the mechanical properties of the pinnules themselves. Passive orientation of comatulid arms

has apparently not been investigated. Alternatively, the constant twist-to-bend ratio of comatulid crinoid arms may reflect functional demands of locomotion. Comatulid crinoids use their arms to crawl along the surface of the reef and to swim freely through the water. Each of these activities place different functional demands on the arms, and these demands may be reflected in the constant twist-to-bend ratios.

The mechanical properties discussed here represent the passive properties of the arms. Crinoids may be able to actively alter the mechanical properties of their arms by contracting the muscles that cross from one ossicle to the next or by making changes in the properties of their connective tissue. As in all echinoderms, crinoid ligaments are made up of catch connective tissue that can exhibit dramatic changes in mechanical properties (Diab and Gilly, 1984; Motokawa, 1984). Crinoids might be able to use muscular contractions to position the arms, and then use the mutable properties of catch connective tissue to maintain that position with little muscular effort (Willkie, 1983). Thus, the ability of a crinoid to feed and locomote may depend on both the passive and active properties of the arms.

The crinoids used in this study were initially preserved in formalin, which increases the number of cross-links between the proteins in connective tissue (Presnell and Schreibman, 1997). Such treatment will greatly influence the mechanical properties of these tissues (Wainwright et al., 1976). The reported values for flexural stiffness are within an order of magnitude of values reported for the stalks of living stalked crinoids (Baumiller and LaBarbera, 1993). Yet the stalks were about 3 times larger in diameter than the comatulid arms, suggesting that the values for the flexural stiffness of arms given here are overestimates of the true values. No values were available for comparisons with torsional stiffness. In the multi-jointed vertebrate spine, the magnitudes of both flexural and torsional stiffness increased after preservation in formalin, yet the twist-to-bend ratio remained the same (Wilkie et al., 1996). Thus, although the magnitudes of flexural and torsional stiffness in preserved crinoids may be overestimates, the twist-to-bend ratios may accurately reflect values for living crinoids.

The factors affecting beam stiffness in crustacean antennae differed in part from those affecting crinoid arms. The flexibility of crustacean antennae is dependent on their diameter but not their joint density, suggesting that these beams effectively function as continuous beams. Increases or decreases in the number of joints in the antennae do not significantly affect their mechanical properties. I suggest that the joints of the antenna are not designed to allow appreciable bending or twisting. Previous studies have shown that the mechanoreceptors on the antenna are sensitive to bending deformations of 0.06 degrees at each joint (Tautz et al., 1981). Thus, the joints may allow only very small deformations. Deformations of this magnitude, if they occurred, were below the resolution of the present equipment.

Both *Procambarus* and *Panulirus* use their antennae to collect sensory information, but *Panulirus* also uses its antennae in aggressive interactions with predators (Atema and Cobb, 1980). The antennae of *Panulirus* do not bend or twist easily, which may make them more effective tools for warding off predators. Yet, because stiffness is related to diameter, the ability to ward off predators may be size dependent. In contrast, the antennae of *Procambarus* deform easily in response to loads, ensuring their sensitivity to environmental stimuli. The twist-to-bend ratios differed significantly, with *Panulirus* having a lower ratio than *Procambarus*. A variable twist-to-bend ratio suggests that flexural stiffness and torsional stiffness are not tightly coupled in the crustacean antenna. This decoupling may be indicative of the different functional demands placed on the two antennae, or alternatively, may simply reflect the functional irrelevancy of torsional stiffness in these structures.

Mechanistically, the decoupling of flexural and torsional stiffness in crustacean antennae may be a function of subtle morphological or material changes that affect one of the stiffness variables to a greater degree than the other. For example, the stiffness of a hollow beam, such as a crustacean antenna, is influenced not only by its external cross-sectional shape, but also by the thickness of its walls (Roark, 1943; Niklas, 1998). This study did not investigate wall thickness or other morphological features within each hollow antenna. Thus, the assumption that the two different antennae have the same structural design may be inappropriate despite their external similarity.

The antennae used in this study were frozen and thawed prior to mechanical tests, which could have affected the results. The flexural stiffness reported for *Procambarus* was very similar to values reported for other similarly sized freshwater crayfish that were tested immediately after death (Sandeman, 1989). For torsional stiffness, no data from fresh specimens were available for comparisons. Again, the values reported here reflect the passive properties of the antennae. In crustaceans, no muscles cross over the joints in the antenna, so there is no possibility of active control of the mechanical properties of the structure.

The mechanical properties of multi-jointed beams do not differ dramatically from those of continuous biological beams, despite large differences in underlying morphology. Both multi-jointed and continuous beams have similar mechanical properties despite vastly different structural designs and functional demands. This convergence suggests that the structural design of a biological beam does not necessarily determine the resultant mechanical properties. This commonality also emphasizes the importance of flexibility, both in bending and in twisting, biological beams.

Acknowledgments

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